

Behaviour and within-habitat distribution of adult *Erebia sudetica sudetica*, endemic of the Hrubý Jeseník Mts., Czech Republic (Nymphalidae, Satyrinae)

TOMÁŠ KURAS¹, JIŘÍ BENEŠ² & MARTIN KONVIČKA²

¹ Department of Ecology, Natural Science Faculty, Palacký University, Tr. Svobody 26, Olomouc, CZ-77146, Czech Republic; e-mail: kuras@risc.upol.cz

² Department of Zoology, School of Biological Sciences, University of South Bohemia, Branišovská 31, České Budějovice, CZ-370 05, Czech Republic; e-mail: Konva@tix.bf.jcu.cz.

Summary. Using quantified observations along a transect route, we studied behaviour, utilisation of habitat patches, and behavioural changes during flight season in the butterfly *Erebia sudetica sudetica* Staudinger, 1861, a potentially endangered high-mountain endemic of the Eastern Sudetes. We constructed a generalised linear model that accounted for over 52.6% of variation in the transect records. Diurnal behaviour followed a distinct temporal pattern: males patrolled in early mornings, both sexes devoted increasing time to nectaring in afternoon hours. A corresponding temporal pattern was found in differences of behaviour early vs. lately in the flight season. Towards the end of flight season, the males flew less and both sexes nectared more, relative to the beginning of the flight season. We suggest that decreasing availability of unmated females in late hours and/or lately in flight period caused the shifts towards a maintenance strategy in behaviour of males. Both distribution and behaviour of the butterflies varied in different sections of their habitat; this variation reflected distribution of adult resources. We observed the majority of egg-laying activities at one of the mown sections, but we can not exclude a recording bias; still, the mowing management, if executed in a patchy manner, probably does not harm the butterflies. We also describe courtship, copulation and egg-laying in *E. sudetica*, and report observational notes on utilisation of nectar plants and predators of the butterfly.

Zusammenfassung. Auf der Grundlage quantitativer Beobachtungen entlang eines Linientransektes analysierten wir Verhalten, Habitatnutzung und Verhaltensänderungen über die Flugzeit hinweg von *Erebia sudetica sudetica* Staudinger, 1861. *E. sudetica sudetica* ist ein potentiell gefährdeter Endemit der hochmontanen Stufe des Altvater-Gebirges (Tschechische Republik). Wir konstruierten ein generalisiertes lineares Modell, das 52.6% der Varianz der Beobachtungsdaten erklärt. Das Verhalten folgte im Tagesverlauf einem deutlichen Muster. Männchen patrouillierten am frühen Morgen, beide Geschlechter zeigten vor allem nachmittags Nektaraufnahme. Ein ähnliches Muster wurde im Vergleich der frühen bzw. späten Flugperiode beobachtet. Am Ende der Flugzeit waren die Männchen weniger flugaktiv, und beide Geschlechter zeigten intensivere Nektaraufnahme, verglichen mit dem Beginn der Emergenz. Wir vermuten, daß die geringere Verfügbarkeit unbegatteter Weibchen am Nachmittag bzw. am Ende der Flugperiode die Ursache dieser Verschiebung zugunsten einer auf Aufrechterhaltung der Körperfunktionen ausgerichteten Strategie der Männchen ist. Verteilung der Tiere im Habitat und Verhalten der Falter variierten zwischen den verschiedenen Habitatabschnitten; dies spiegelte die Verteilung der adulten Ressourcen wider. Wir beobachteten die Mehrheit der Eiablagen in einem gemähten Teilabschnitt des Transekts, können aber einen Bias durch unsere Datenaufnahme nicht ausschließen. Habitatmanagement durch fleckenhafte Mahd beeinflusst die Population vermutlich nicht negativ. Wir beschreiben darüber hinaus Balz, Paarung und Eiablageverhalten von *E. sudetica*. Beobachtungen zur Nektarpflanzennutzung und zu Prädatoren werden ebenfalls dargestellt.

Resumé. Sur base d'observations quantitatives au long d'une route fixée, nous avons étudié le comportement, l'utilisation de l'habitat ainsi que les modifications du comportement au long de la période de vol, d'*Erebia sudetica sudetica* Staudinger, 1861, endémique menacé de haute montagne de l'est des monts des Sudètes. Nous avons élaboré un modèle linéaire généralisé qui explique 52.6 % de la variation des données du transect. Le comportement diurne suivait un modèle temporel distinct: les mâles patrouillaient en début de matinée et les deux sexes consacraient plus de temps à l'alimentation l'après-midi. Un modèle temporel similaire a été trouvé au niveau de différences de comportement au début par rapport à la fin de la période de vol. Vers la fin de la période de vol, les mâles volaient moins et les deux sexes se nourrissaient plus fréquemment, comparativement au début de cette période. Nous suggérons qu'une disponibilité réduite.

Key words. *Erebia*, ringlets, alpine butterflies, diurnal behaviour, temporal patterns, generalised linear model, mate-location strategies, conservation management.

Introduction

Erebia sudetica (Staudinger, 1861) is a European species of global conservation concern, owing to its highly restricted distribution (Cupedo 1995; Van Swaay & Warren 1999). Its several subspecies occur discontinuously in a few mountain areas (Cupedo 1997), of which the Hrubý Jeseník Mts. (= Altvater, Eastern Sudetes, Czech Republic) are inhabited by the nominal subspecies *E. sudetica sudetica*. It forms there a system of relatively sedentary colonies in wet, floristically rich sites near timberline.

This study, a part of comparative research of *Erebia* satyrines in the Hrubý Jeseník Mts. (related papers, e.g., Beneš *et al.* 2000; Kuras *et al.* 2000; Kuras, Konvička *et al.* 2001), focuses on adult behaviour and within-habitat distribution of *E. sudetica*. During a parallel work on two related species, *E. epiphron silesiana* Meyer & Dür, 1852 and *E. euryale euryale* (Esper, 1805), we found 1) that micro-distribution of the two species differed in relation to micro-habitat patterns even in sympatry, and 2) that diurnal activity of both satyrines followed a clear diurnal pattern. The males tended to patrol in morning hours, whereas both sexes devoted afternoons mainly to nectar-feeding. The latter observation was expected on the basis of maximising male fitness in a species, in which females emerge early in the morning (cf. Kuras, Beneš *et al.* 2001) and the males benefit from mating with fresh females. However, existence of a diurnal rhythm of activity was never mentioned for any *Erebia* species (e.g. Brussard & Ehrlich 1970; Porter & Emmet 1989; Kirkland 1995). On the contrary, Ikejiri *et al.* (1980) proposed that behavioural schedule of mountainous representatives of that genus should not be governed by time of day, but should be rather opportunistic and closely tied to momentary weather. Such opportunism should allow the butterflies to respond rapidly to changing external conditions and to utilise most of the time when weather is favourable for flight and reproduction.

We aim to contribute to resolving the above contradiction by quantifying diurnal behaviour of another mountainous *Erebia*. Besides, we provide additional observations on the adult life history of this little-known species, and investigate possible impacts of recent management of the locality, which is one of the largest existing colonies of *E. sudetica* in the entire mountains. The management consists of patchy mowing that seeks to mimic traditional, long-abandoned grazing/hay-making. We included two of the mown patches into the study.

We first construct a statistical model, based on quantified observations along a transect route, in order to explore the effects of time of day, weather, and vegetation structure on behaviour of the butterfly. We specifically ask (a) whether there is any detectable diurnal pattern in activity of *E. sudetica*; (b) how is the distribution of adults of *E. sudetica*, and their respective behaviour, related to within-habitat structure of vegetation, including the recent mowing management.

Methods

Study site, field work. – We established a line transect across the largest colony of *E. sudetica* in the area of interest, which is situated at the tall-herb alpine grasslands of the glacial cirque Malá Kotlina, Hrubý Jeseník Mts. (50°02' N, 17°12' E, ca 1250 m alt.).

In the year of the study, total adult recruitment was ca 4500 individuals, and the flight period lasted from July 18 until shortly after August 16. The locality is one of the floristically richest in the mountain system of Eastern Sudetes. The timberline is naturally depressed there as a result of avalanche-caused disturbances. The site had been grazed until World War II, now it is protected as reserve. The experimental mowing began a decade ago.

It was not feasible, due to the rugged terrain of the habitat with steep slopes and waterlogged sites, to cover the entire site of the studied colony by our transect route. We thus established one short transect (100 m) that nevertheless included all distinct types of vegetation inhabited by the butterfly. It was divided into 7 sections defined by overall characters of vegetation.

These were: (1) A section with species-poor *Molinia* grassland, low abundance of potential nectar sources, length 15 m. (2) Experimentally mown dry patch, a higher cover of short grasses (*Festuca* spp., *Nardus stricta*, *Avenella flexuosa*), low supply of nectar sources, length 15 m. (3) A 'ruderalised' site, possibly due to influx of nutrients from dumping of biomass from mowing. Extended patches of *Senecio nemorensis* agg. were the principal nectar source; length 10 m. (4) Experimentally mown wet patch, high cover of *Phalaroides arundinacea*; length 10 m. (5) Wet site with numerous springs, high abundance of flowering plants with prevailing *Allium schoenoprasum*; length 20 m. (6) A shady section with scattered dwarf spruces, high abundance of *Senecio nemorensis*; length 10 m. (7) A partially shady section with scattered trees and herbaceous vegetation with a high density of species typical for a spruce climax forest understory (*Luzula sylvatica* and *Vaccinium myrtillus*), but still rich in nectar sources including *Senecio nemorensis*; length 20 m.

We walked the route on July 19, 20 and August 1, 6, 7, 1998, attempting to cover entire days and counting all individuals of *E. sudetica* and their behaviours at the moment when we spotted them. For each walk, we recorded the following variables: Hour, Temperature (ambient temperature prior to walk), Sunlight (estimated on 4-point scale, 1 being overcast, 4 fully clear sky), and Wind (3-point relative estimate). The categories of butterfly activities were: 'Patrolling' (if males), 'Flight', 'Nectaring' (including feeding on mud, sweat etc.); 'Basking', 'Resting', 'Mating', 'Oviposition', and 'Chasing'.

Because the data were collected by repeated observation along a single transect, we are aware that they do not constitute true replications. However, the design used was the only plausible way to assess diurnal changes of behaviour of the butterfly, given its highly restricted distribution and the nature of the terrain. In analysing the data, we at least partially ameliorate this problem by considering individual transect walks and dates as co-variables. We thus applied more stringent criteria for assessing significant effects of the independent variables of interest.

Statistical analyses.

Because the potential explanatory variables were of both categorical and continuous nature, we employed generalised linear modelling (= GLM) to detect their effects on numbers of recorded butterflies. GLM procedures fit the response variables as linear functions, called link-functions, of the explanatory variables, which may be both cat-

egorical and continuous. Goodness of fit of the fitted models is assessed by analysis of deviance, which is defined as the difference between the maximum fit of a model in which the fitted values are identical with the observed values, and the log-likelihood of the values predicted by the model tested.

We constructed the model using the S-plus program package (S-Plus 2000, 1999). Since our response variables were counts of individuals, we used Poisson's regressions with the log link-function. Our response variable was the number of individuals per walk/section split into sexes and classes of observed behaviours. (These were as above with the exception that we included the 'Chasing' and 'Patrolling' under 'Flight' and collapsed 'Oviposition' and 'Mating' into 'Reproductive' behaviour.) The explanatory variables were Section, Sex, Hour, Sunlight, Wind, Temperature, and Period, the last one denoting the beginning (the July walks) vs. end (the August walks) of the flight season. We also considered three additional variables with potential influence on the variation in our data: the day of observation ('Date'), the identity of a transect walk ('Transect'), and the length of transect section ('Length'). Since effects of these variables were not of interest in our hypotheses, we worked with them in the same manner as with co-variables in analysis of variance, considering significance of all explanatory terms after including the effects of the three co-variables into the models.

In building the model, we first defined two null models, NULL and NULL-COV, the latter containing the three co-variables. Then, because GLM procedures assume linear responses of a fitted variable to predictor variables and we had no a priori knowledge regarding the shapes of response curves, we controlled for possible non-linear interactions by fitting a generalised additive model (GAM) with all potential explanatory variables. We used the S-plus 'step.gam' procedure for model selection, entering each of the explanatory variables (if appropriate) in linear, quadratic and cubic alternatives. Next, after testing independent single-factor effects of all potential explanatory variables (including co-variables) by procedures corresponding to single term regressions (or ANOVAs), we constructed three 'saturated' models. These included all the potential explanatory variables (FULL-1), plus all their second- (FULL-2) and third- (FULL-3) order interactions. Such higher-order models typically explain large amounts of variation in data, but their utility for interpretation is limited due to their complexity. We used them as templates, against which we compared all simpler models that we constructed further.

We built the simpler models iteratively, based on results of analyses of deviance of all terms included in the saturated models. In cross-evaluations of alternative models, we considered the values of Akaike's information criterion (AIC), a statistics that weighs increasing explanatory power of more complex statistical models against their increasing complexity, penalizing models that are too complex (S-Plus 2000, 1999). We kept adding and/or deleting all nominally significant terms, until it was not possible to attain, by either of the procedures, any model with better performance than our final model (BEST). If we encountered some interactions of 2 (3) factors that were nominally significant and improved the fit of the model, but contained nominally non-significant single-factor terms, we included also the single-factor terms into the model.

Results

Model construction. – We performed 69 walks and obtained 1011 behavioural records (513 males, 498 females: a not significant deviation from 1:1 ratio with $\chi^2_{1df} = 0.12$ and $p = 0.72$). Proportions of sexes differed between the July and August transects walks, with males prevailing in July (249 ♂♂, 90 ♀♀; $\chi^2_{1df} = 8.46$, $p < 0.001$) and females in August (264 ♂♂, 408 ♀♀; $\chi^2_{1df} = 15.61$, $p < 0.001$).

All single factors except Length, Sex, Wind and Temperature significantly influenced variation in the transect data (Table 1). After including the factors Length, Date and Transect as co-variables, the significant effect of Sunlight was lost, presumably as a result of collinearity between the amount of insolation and individual dates and/or transects walks. A plausible interpretation of the absence of a significant effect of the factor Length is that its effect on butterfly numbers was suppressed by biologically relevant differences among individual sections. (If raw counts of butterflies per section, disregarding the behaviours, were analysed by one-way ANOVA with Length as co-variable, the effect was highly significant: $F = 5.76$, d.f. = 1,6, $p < 0.0001$). To control for the possibility that the lack of significance of the factor Temperature was caused by inflated degrees of freedom (due to missing measurements for 1 day of recording, cf. Table 1), we repeated the linear regression only for the walks for which the temperature records were available. The result was again not significant ($\beta = 0.0026$, $R^2 = 0.00003$, $F_{1,3778} = 0.14$, $p = 0.71$).

About one fifth of the variation in the recorded data was attributable to the co-variables (Table 2). The model GAM included the factors Date, Transect, Behaviour, Section and Wind, plus the quadratic effect of Hour. It explained about the same proportion of variance as the model FULL-1. The portions of explained variance increased after including all possible two-factor terms, but still growing complexity resulted into unacceptably high values of AIC (FULL-3 model).

After subtracting the variation due to co-variables from the model BEST (Table 3), it explained about 30% of variance in the data. Whereas the significant contributions of some of the terms, such as Behaviour, were trivial (different behaviours were observed in different frequencies), several of the included terms carried profound biological implications.

Differences between sexes. – Males flew more frequently than females. Relatively more basking and nectaring records came from the female sex. The pattern was similar to all the mountainous *Erebia* studied so far, in which the males seek for their mates by active patrolling (Brussard & Ehrlich 1970; Scott 1974; Porter & Emmet 1989; Bayfield & Taylor 1994). Considering the frequent basking of females, it should be recalled that their egg-laying activity is both energy demanding and occurs in relatively cool conditions near the ground. The females thus presumably intersperse oviposition with frequent basking, even in warm mid-days, to regain temporarily lost heat.

Temporal patterns. – Numbers of recorded butterflies and their activities varied with the time of day (Fig. 1). The pattern was further influenced by sunlight. In sunny conditions, the butterflies were active since ca 8 am until before 6 pm (C. European summer time). There was a clear peak in flight (i.e. patrolling) activity of males be-

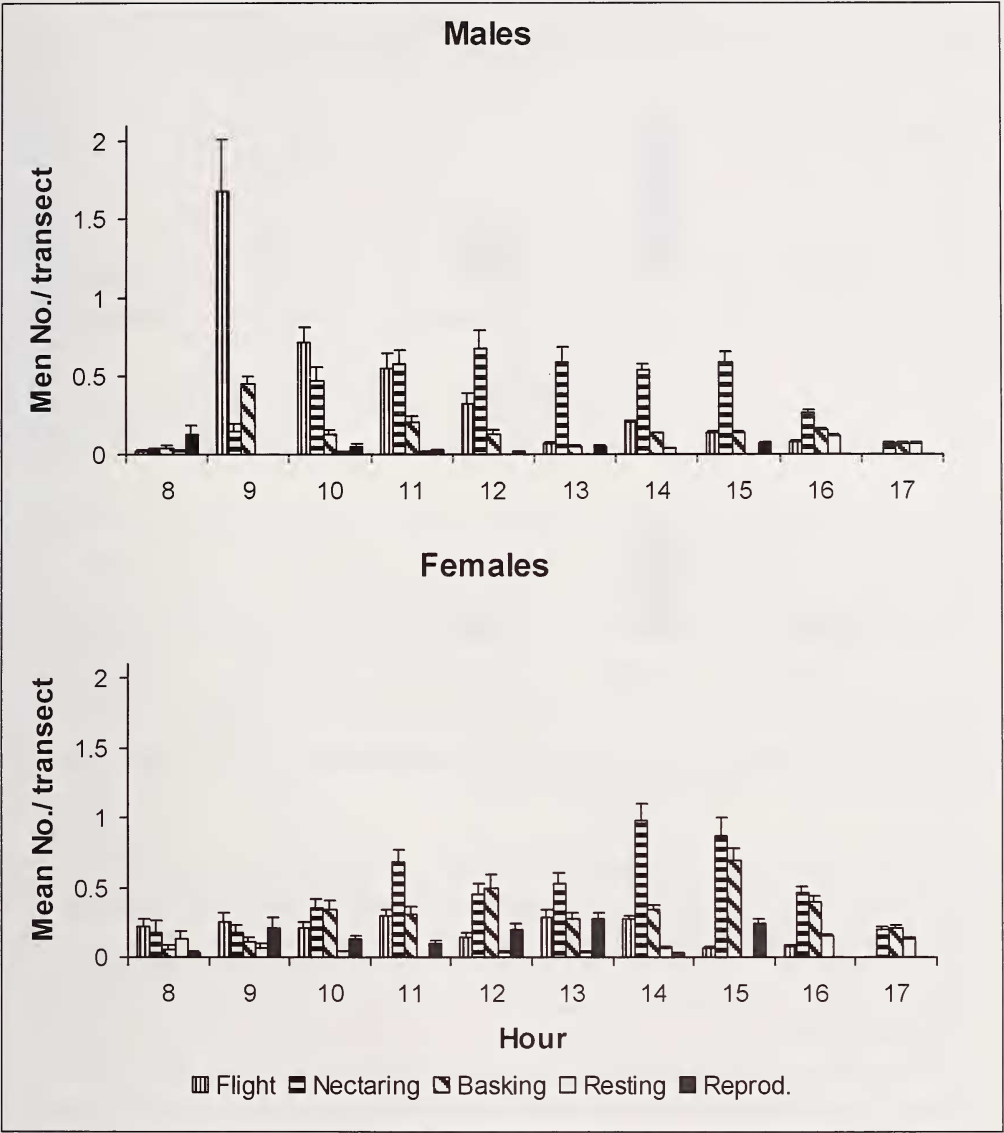


Fig. 1. Diurnal changes of behaviour of *Erebia sudetica sudetica* observed along a transect route in the Hrubý Jeseník Mts.

tween 9 and 10 am, whereas nectaring was the most frequent activity of both sexes in afternoons. In late afternoons, both sexes increasingly basked, and eventually rested. We typically observed resting on patches of long-bladed grasses, such as *Molinia coerulea* *Phalaroides arundinacea*. The butterflies spent nights at such sites, often in loose aggregations as described for *Erebia* spp. by Schwarz (1949) and Ribaric & Gogala (1996).

Activities of the butterflies further differed between the beginning (July records) and the end (August records) of their flight season (Fig. 2). Lately in the season, when there

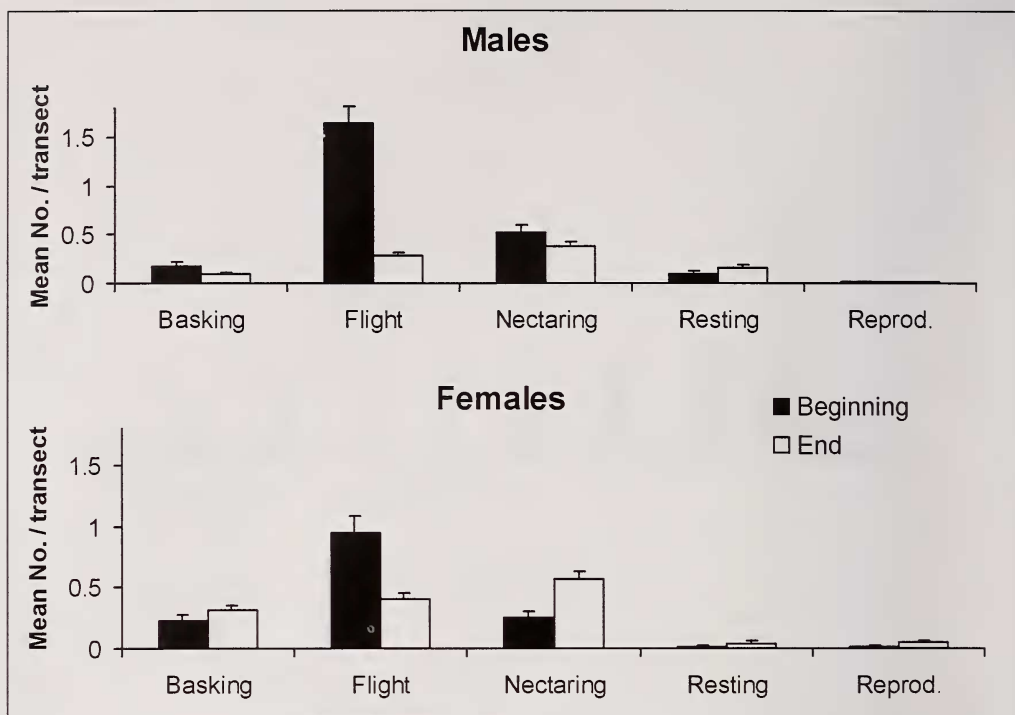


Fig. 2. Changes of relative proportion of activities of adults of *Erebia sudetica* in the beginning (July 1998) vs. in the end (August 1998) of its flight season.

were relatively fewer males and more females present (i.e. the significant term Sex \times Period), both sexes flew less frequently, and fed on nectar more frequently, relative to the beginning of flight season.

Vegetation structure. – As indicated by the significant contributions of the terms Section, Section \times Behaviour and Section \times Hour² to the BEST model, distribution of the butterflies (and of their behaviours) was influenced by vegetation of the sites (Fig. 3). Records of feeding of both sexes prevailed at the sections with large patches of flowering *Senecio nemorensis* (3, 6). The males (prevailing on the July transects) nectared in large numbers at the section (5), which contained copious stands of *Allium schoenoprasum* (already senescent in August). The basking and resting records were centred at patches with long-bladed grasses (1, 4, 6). Records of 'Reproductive' behaviour, represented primarily by egg-laying in females, dominated on the mown section (2). These patterns were further influenced by changing insolation of individual sections during the days, as indicated by inclusion of the terms Section \times Hour² \times Sunlight and Hour² \times Behaviour \times Sunlight to the BEST model.

Observational notes. Mating. – Courtship is initiated by landing of a patrolling male next to a female. Both sexes then flap for ca 5 seconds with their antennae close to the other butterfly's body. The male is very active in this phase, moving around the female and flapping with his wings. If a courtship results in mating, the couple assumes a vertical position with the female above the male as the pair-carrying sex.

Tab. 2. Summary of the procedures of selecting the most appropriate model fitting the transect data on behaviour and distribution of *Erebia sudetica sudetica*. Fit of each of the successive models was tested against the null model (NULL). See Methods for details.

Model	Residual D.f.	Residual deviance	Model D.f.	Model deviance	AIC	F	p	Explained variance (%)
NULL	4739	5110.3			5111.4			
NULL-COV	4667	3948.2	72	1162.0	4162.0	11.0	< 0.001	22.74
GAM	4655	3171.2	84	1939.0	3465.2	13.3	< 0.001	58.24
FULL-1	3698	2133.7	1041	2976.6	5510.7	1.8	< 0.001	58.25
FULL-2	3584	1571.8	1155	3538.5	3861.7	3.1	< 0.001	69.24
FULL-3	3186	9140.5	1553	9140.5	10987.6	4.4	< 0.001	N.A.
BEST	4569	2420.7	170	2689.6	2781.2	15.0	< 0.001	52.64

We dissected 15 wild-captured females and found only a single spermatophore in the bursa copulatrix of each of them. However, the small sample does not allow us to exclude rare instances of repeated insemination, as they were reported for other *Erebia* species (Ehrlich & Ehrlich 1978; Mansell 1982; Kuras, Beneš *et al.* 2001). Indeed, we obtained indirect evidence of repeated insemination in *E. sudetica* in the context a mark-recapture study (Kuras *et al.* unpublished). We encountered *in copula* two females, which were previously individually marked and which were minimally 2 and 4 days old. Regarding males, we encountered 4 previously marked individuals while mating; they were minimally 1, 4, 5, and 12 days old (Table 4).

Oviposition. – It is a relatively quick act, during which a female lands on the ground, ‘runs’ back and front for a few seconds obviously exploring the substrate, and then bends her abdomen and releases one egg. We recorded the majority of egg-laying acts at the mown site (2) (Fig. 3) with a high cover of short-tuft grasses, which are the larval foodplants (Kuras, Beneš *et al.* 2001). However, we could observe the activities in detail only at this site, and we cannot be certain whether the females actively preferred such shortly trimmed substrates, or whether this was a recording artefact. We found deposited eggs on both living and dead leaves at the base of grass tufts up to 5 cm above the ground (Table 4).

Adult feeding. – At the study locality, the butterflies fed on a wide range of flowering plants. The diversity of nectaring records reflected the high floristic richness of the Malá Kotlina cirque. We did not test for nectar feeding preferences, and give the following list only for illustrative purposes. In descending order of frequency, the visited nectar plants along the transect were (N = 439): *Senecio nemorensis* agg. (75.2 %), *Scabiosa lucida lucida* (5.6%), *Allium schoenoprasum alpinum* (6.6%), *Crepis sibirica* (4.3%), *Potentilla erecta* (3.3%), *Pilosella aurantiaca*, *Dianthus superbus alpestris*, *Pimpinella saxifraga*, *Ranunculus lanuginosus*, and *Scorzoneroidea autumnalis* (each < 3%). Besides these species, the butterfly frequently visited other plant species in the Hrubý Jeseník Mts., most notably *Adenostyles alliaria*, *Laserpitium archangelica* (this one often after rains), *Solidago virgaurea alpestris*, *Trommsdorffia uniflora*, *Bistorta major*.

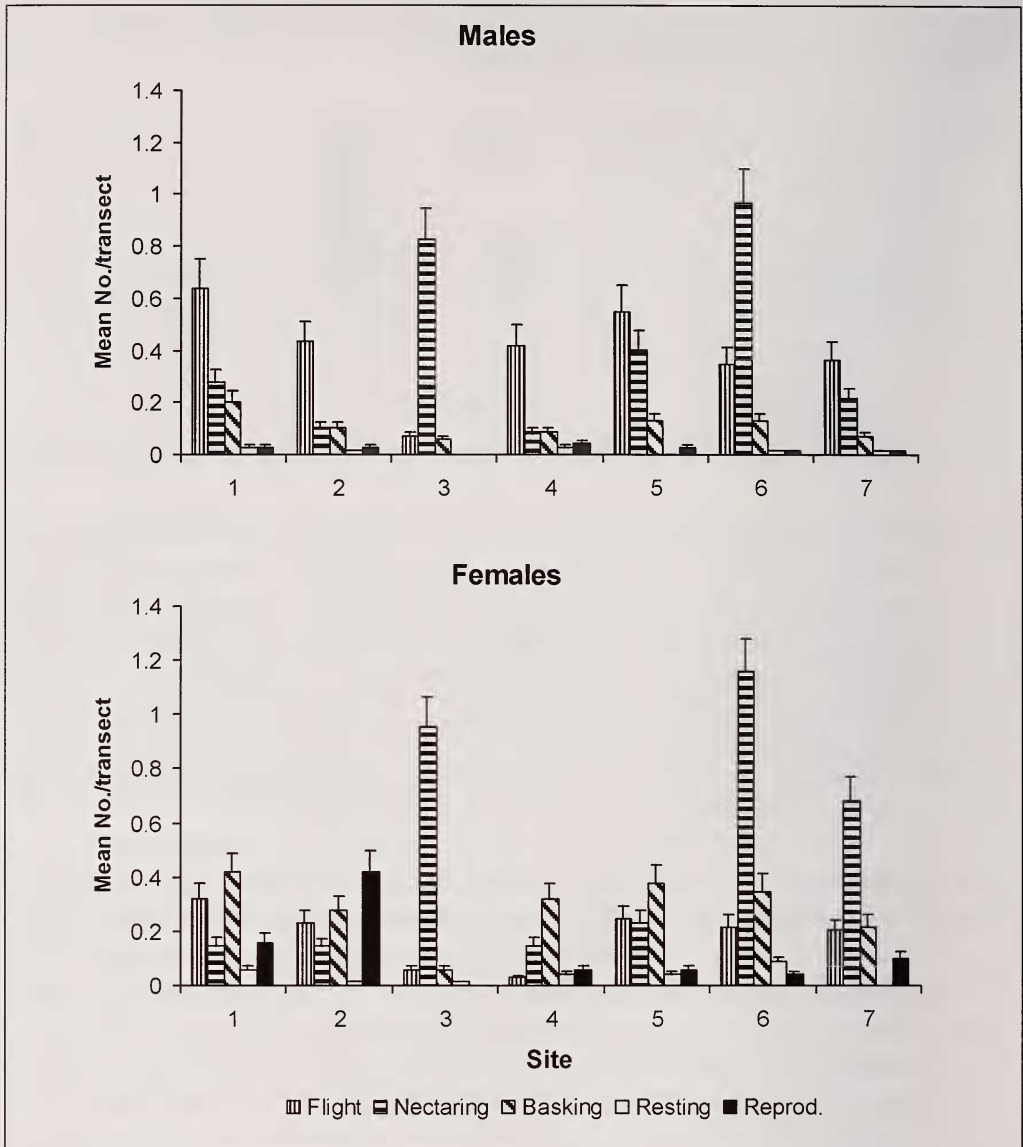


Fig. 3. Distribution of different types of behaviour of adults of *Erebia sudetica sudetica* along different sections of a fixed transect route. See Methods section for description of the sections.

Both sexes often puddled on a humid bare ground, or even on our sweat-covered bodies. Wocke (1850) noted frequent sucking on livestock excrements in times when the alpine elevations of the Hrubý Jeseník Mts. were extensively grazed.

Predation. – We observed three unsuccessful attacks by the common lizard (*Zootoca vivipara*) on basking/egg laying females. One sub-adult robin (*Erithacus rubecula*) obviously specialised on preying on the butterflies at our site (3). Finally, we found 8 butterflies captured in nets of the spider *Aculepeira ceropegia* (Walckenaer, 1802). We analyse the frequencies of marks of unsuccessful attacks by predators in the population

of *E. sudetica* elsewhere (Kuras *et al.* in press). Bureš (1994) reported *Erebia* adults in the diet of meadow pipit nestlings from the same area.

Tab. 3. Summary of the model BEST, used for fitting the transect observations of behaviour and distribution of adults of *Erebia sudetica sudetica*.

Term	D.f.	Deviance	Resid. D.f.	Resid. Deviance	F	p
(Null)			4739	5110.3		
Length	1	0.03	4738	5110.2	0.03	0.86
Date	4	317.8	4734	4792.4	75.4	< 0.001
Transect	67	844.2	4667	3948.2	12.0	< 0.001
Behaviour	4	706.7	4663	3241.6	167.6	< 0.001
Period	0	0.00	4663	3241.6	N.A.	N.A.
Sex	1	0.3	4662	3241.3	0.2	0.63
Section	5	41.0	4657	3200.3	7.8	< 0.001
Hour ²	2	27.0	4655	3173.3	12.8	< 0.001
Sunlight	1	0.1	4654	3173.3	0.1	0.8269
Sex×Period	1	51.8	4653	3121.4	49.2	< 0.001
Hour ² ×Behaviour	8	81.8	4645	3039.6	9.7	< 0.001
Period×Behaviour	4	55.1	4641	2984.5	13.1	< 0.001
Behaviour×Sex	4	79.2	4637	2905.4	18.8	< 0.001
Behaviour×Section	24	325.2	4613	2580.2	12.9	< 0.001
Section×Hour ²	12	34.7	4601	2545.6	2.7	< 0.01
Section×Sunlight	6	27.5	4595	2518.1	4.4	< 0.001
Behaviour×Sunlight	4	21.5	4591	2496.6	5.1	< 0.001
Section×Hour ² ×Sunlight	14	31.1	4577	2465.5	2.1	< 0.01
Hour ² ×Behaviour×Sunlight	8	44.8	4569	2420.7	5.3	< 0.001

Tab. 4. Summary of observational records of reproductive activities of *E. sudetica sudetica*.

Activity	N	Mean duration (SD)	Time of day	Substrate
Copulation	7	35 (8.9) min	8:45 - 16:10	Grass tufts (8)
Copulation*	3	38 (6.4) min		Flowers (2)
Egg laying	47**	"10 - 30 seconds"	9:30 - 15:00	<i>Avenella flexuosa</i> (11) <i>Deschampsia caespitosa</i> (6) <i>Nardus stricta</i> (4)

* These copulations were observed since the beginning to end.

** We actually found the eggs only in 21 cases.

Discussion

Behaviour. — We showed that diurnal behaviour of *E. sudetica* followed a well-defined pattern and that the behaviours observed along the transect differed between first and second half of flight season. Moreover, the seasonal pattern reflected the pattern observed on within-day basis.

On the during-day basis, patrolling flights of males prevailed in mornings, whereas nectaring of both sexes culminated in afternoons. In this respect, the diurnal rhythm of *E. sudetica* was practically identical to that found for related *Erebia epiphron* and *E. euryale* (Konvička *et al.* unpublished). In the three species, and probably also in *E. aethiops* (discussed in Lear 1989), the males presumably maximise their mate-locating effort in early morning hours, which is the eclosion time of females in that group of butterflies (Porter 1989; Lear 1989; Kuras, Beneš, *et al.* 2001). This strategy of males supports the prediction of Odendaal *et al.* (1985), according to which males should maximise searching effort at the time when a majority of fertilisable females is available. It also agrees with the model of Ide & Kondoh (2000), according to which males should change their mate-locating strategy if the expenditures invested to pursuing females prevail over fitness advantages from obtaining one.

The case of *E. sudetica*, however, differs from the situations modelled by Ide & Kondoh (2000) in one aspect: whereas the authors primarily considered switches of mate-locating tactics (such as patrolling vs. perching in Wickman 1985), we document here rather a non-effort on the side of males towards afternoons. Because no variant of a 'sit-and-wait' strategy was ever documented in the genus *Erebia*, evolutionary constraint on the existence of such an alternative to patrolling is the most plausible explanation of the difference. Indeed, under such a constraint, the declining flight activity and increasing concentration on nectaring represents exactly the alternative opened to males as soon as fertilisable females become scarce.

The afternoon decline of patrolling of males does not, however, entirely exclude the possibility of mating lately in the days; indeed, we observed one copulating pair at about 4 pm (Table 4). This does not conflict with the above reasoning. First, even if we had assumed that all females emerged early in the days, and that all newly eclosed females obtained their partners quickly after emergence (both assumptions are realistic, but there is no reason why exceptions should not exist), our finding of at least two old females *in copula* suggests that males occasionally mate with non-virgins females. Second, our data suggest that the decreased patrolling activity of males in afternoons was rather due to progressive alternation of flight with 'maintenance' (i.e. nectaring), than due to an abrupt change of activity. Rutowski (1991) suggested exactly such pattern as suitable for species in which males are sexually active for whole days.

Indeed, the progressive afternoon shift towards nectaring may provide the best strategy for the males, if we realise that their potential mates stay in vicinity of nectar plants for most of days (with the exception of the freshly eclosed virgins in the mornings). This effectively shifts the distribution of potential encounter sites of the sexes from the places where the females eclose (which is practically 'anywhere' under the foodplants, promoting the patrolling strategy) to patches that contain adult resources. Hence, the males that

feed on nectar in the afternoon both maximise their chances to meet a female that may be will copulate, and, by replenishing energy supplies, increase their potential survival.

The relative value of surviving to a next day may indeed be very high in *Erebia sudetica*. We show elsewhere (Kuras *et al.* unpublished) that the butterfly is markedly protandrous: the peak emergence of males preceded the peak of females by about a week in 1998. It is also relatively short-living, reaching average residences of 3–4 days, although the maximum recorded residence of a male was 15 days, and some males may mate at an old age. Because fresh females in such a species keep appearing even when the majority of males have already eclosed, we propose that the portion of males that achieves a prolonged residency may gain disproportional fitness advantage, thus selecting for a ‘frugal’ maintenance strategy.

Perhaps the most important finding was the striking parallel between the diurnal rhythm and the behavioural shift that we observed on a seasonal basis. Obviously, the changes were related to progressive ageing of the population. In a protandrous population, each individual is ageing into a world characterised by decreasing proportion of males and decreasing supply of virgin females. These facts predict exactly the same changes in activity of sexes lately in flight season as lately during individual days. Namely, both the late-season males and females should spend relatively less time in flight and more time with nectaring, which indeed was the case. An average male should devote increasing amount of time to feeding not only in order to replenish resources, but also because there are relatively few virgin females around, and thus a higher proportion of fertilisable females is likely to be found at flowers. Moreover, decreasing competition among the males (as a result of declining numbers) should relax the necessity to invest into patrolling flights.

The seasonal shift in behaviour documented here, although reasonably justified on the basis of relative advantage of active mate-locating by flight vs. a passive maintenance strategy, may be a widespread but overlooked phenomenon in butterfly biology. However, it may be relatively common; the above reasoning predicts its widespread occurrence in protandrous species that are either univoltine, or occur in discrete generations. Notably, shifts in mate-locating strategies were occasionally observed in the context of studying other phenomena (e.g. Shreeve 1987). The phenomenon deserves to be further explored, as it may, for instance, distort some results of mark-recapture studies. On the other hand, some of the vast amount of mark-recapture data accumulated by lepidopterists may be well suited for studying this seasonal shift in adult activity, because such data typically include records of behaviour prior to capture and wing wear of individuals. Therefore, they might allow statistical separation of the effects of individual age from the effects of phenological ‘age’ of entire populations.

Relation to weather. – We did not document any profound relation between activity of the butterflies and temperature. This was perplexing, since temperature crucially affects behaviour of several satyrines (e.g. Heinrich 1985; Wickman 1986), including species of the genus *Erebia* (Brussard & Ehrlich 1970; Konvička *et al.* unpublished). We explain this by the fact that the summer 1998 was unusually warm, with little variation in temperatures recorded while walking the transects (mean 17.73°C, median = 18, range = 14 – 21, SE = 0.026). Thus, we likely collected our data in condi-

tions that were nearly ideal for *E. sudetica* activity. This likely eased our position in documenting the above diurnal/seasonal patterns, but prevented us from answering the question whether the pattern would remain under less favourable conditions more typical for mountain habitats. We expect, however, that the behaviour should be more opportunistic under worse weather, since strictly following a daily rhythm would be too risky from the point of view of an individual's reproduction.

Conservation management. – Our results did not indicate that the mowing of patches of the habitat would harm the endangered butterfly. Rather contrarily, we saw a high number of ovipositions at one of the mown sections, and although we can not exclude a recording artefact, it was clear that *E. sudetica* did not actively avoid such patches. On the other hand, our results suggest that the butterfly requires diversified habitat structure with flowery patches for nectaring and patches of tall-bladed grasses for overnight resting. Therefore, a mosaic-like hay mowing management seems to be appropriate for the colony, provided that it preserves all distinct kinds of vegetation recently present.

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